

DESCENDING INFLUENCES ON THE CUTANEOUS RECEPTIVE FIELDS OF POSTSYNAPTIC DORSAL COLUMN NEURONES IN THE CAT

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SUMMARY

1. The influence of activity in descending systems on the cutaneous receptive field properties of postsynaptic dorsal column (PSDC) neurones has been investigated in chloralose-anaesthetized cats. The main aim of the study was to determine whether the receptive field boundaries of PSDC neurones are under the control of systems descending from the brain.

2. Single-unit recordings were made from the ascending axons of PSDC units in the dorsal columns. Receptive fields were analysed using light tactile and noxious mechanical and thermal stimuli, both before and during a reversible block of spinal conduction produced by cooling the cord rostral of the recording site.

3. The light tactile excitatory fields of PSDC neurones were largely unaffected by the cold-block procedure.

4. In contrast, both the sensitivity of PSDC neurones to noxious stimuli and the area of skin from which they could be effectively excited by such stimuli were found to be profoundly modified by interruption of descending activity. Two-thirds of the units excited by noxious pinch responded more vigorously in the cold-blocked state and one-half from an expanded area of skin. Responses to noxious radiant heat were similarly modified.

5. Inhibition evoked in PSDC neurones, whether by light tactile or noxious stimuli, involved predominantly segmental mechanisms since it remained effective in the cold-blocked state.

6. It is concluded that neurones of the PSDC system are amongst those dorsal horn neurones with receptive field geometries which may be modified by activity in descending systems.

INTRODUCTION

Neurones in the dorsal horn of the spinal cord may be influenced by a variety of systems descending from the brain, some of which are tonically active in animals prepared for electrophysiological recording (see for example Wall, 1967; Brown,

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1971). It is now well established that these descending systems may profoundly modify the response modalities of dorsal horn neurones (Hillman & Wall, 1969; Handwerker, Iggo & Zimmerman, 1975; Dickhaus, Pauser & Zimmerman, 1985) including identified neurones of the spinocervical tract (Brown, 1971; Cervero, Iggo & Molony, 1977).

There is also evidence that descending systems may influence the receptive field geometries of certain neurones (Wall, 1967; Hillman & Wall, 1969). Neurones of the spinocervical tract are considered to be relatively free of such actions (Wall, 1967; Brown, 1971) but little is known of the influence of descending systems on the receptive fields of other ascending tract neurones. Recent electrophysiological studies of identified neurones of the postsynaptic dorsal column (PSDC) system (Noble & Riddell, 1988) have shown that many units have receptive fields consisting of complexly arranged excitatory and inhibitory components. Some PSDC neurones have an extensive subliminal fringe (Brown & Fyffe, 1981) and a minority are reported to have receptive fields that expand following such procedures as electrical stimulation of peripheral nerves (Brown, Brown, Fyffe & Pubols, 1983). These properties suggest that PSDC neurones may be amongst those cells in the dorsal horn with receptive fields under the control of descending systems and the experiments described in this paper were aimed at investigating this possibility. A preliminary report of the results has been published (Noble & Riddell, 1985).

METHODS

Preparation

Experiments were performed on eleven cats (2.1–2.6 kg weight) anaesthetized with chloralose (70 mg/kg) after induction with halothane in an oxygen and nitrous oxide mixture. The adequacy of anaesthesia was assessed by frequent inspection of pupil diameter and of a continuous arterial blood pressure recording. Supplementary doses of chloralose (50–100 mg) were given as required. The cats were intermittently paralysed with gallamine triethiodide and artificially respired. End-tidal CO_2 was maintained at about 4% and rectal temperature at 38 °C. Electrophysiological recordings were discontinued if the mean blood pressure fell below 80 mmHg.

Electrical stimulating and recording procedures

A diagrammatic representation of the preparation on which are indicated the positions of stimulating and recording electrodes is shown in Fig. 1. The spinal cord was exposed by laminectomies performed at C1–C4, Th11–L1 and L3–L7 inclusive. The dorsal columns were sectioned at C1–C2 using watchmakers' forceps; the lesion being extended gradually until the initial negative component of a cord dorsum potential recorded at L7, in response to stimulation of the dorsal columns above the site of transection, was abolished (see Brown, Noble & Riddell, 1986). Bipolar silver-ball electrodes were used to apply search stimuli (3 V, 250 μA , 0.1 ms once every 600 ms) to the dorsal columns at C2 below the lesion, and extracellular recordings made from axons in the dorsal columns at L4–6 using glass capillary microelectrodes containing 4 M-NaCl with impedances of 15–20 M Ω .

Identification criteria

Postsynaptic dorsal column fibres were differentiated from primary afferent fibres by a convergence of cutaneous afferent input and/or by an irregular, bursting background activity. All postsynaptic units were shown to project at least to upper cervical levels by antidromic activation from an electrode on the dorsal columns at C2–3. Antidromic impulses were identified by both collision with orthodromic impulses and by their ability to follow trains of stimuli of at least

500 Hz. The dorsal columns are also known to contain fibres descending the spinal cord (Dart, 1971; Enevoldson & Gordon, 1984). Contamination of the sample of PSDC axons was avoided by the lesion of the dorsal columns which prevented postsynaptic activation of descending fibres.

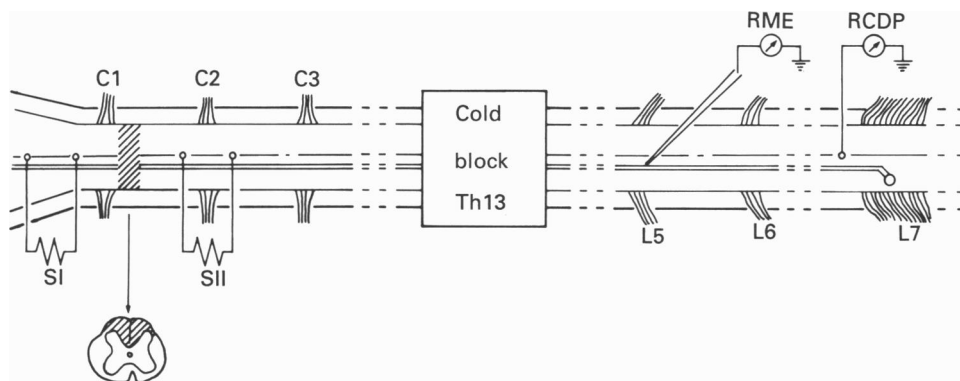


Fig. 1. Schematic diagram of the experimental arrangement showing a plan view of the exposed spinal cord, the locations of stimulating and recording electrodes and the position of the cold-block device. SI and SII represent stimulation sites on the dorsal columns above (C1) and below (C2) a lesion of the dorsal columns at C1-2 (indicated by hatching). RME, recording microelectrode; RCDP, cord dorsum recording electrode.

Reversible block of conduction in the spinal cord

A reversible block of the conduction of impulses through the spinal cord was achieved by cooling a region of cord using a thermoelectric thermode with a cooling surface shaped to surround the dorsal half of the spinal cord (see Brown, 1971). A thermocouple junction mounted on the cooling surface was used to monitor its temperature throughout the cold-block procedure. The thermode was lowered over the Th13 segment taking care to avoid exerting pressure on the cord; the cord dorsum potential recorded at L7 in response to stimulation of the dorsal columns at C2 was monitored for signs of impaired conduction past the thermode during this procedure.

The thermode produced a cold block of the cord within 5–10 min at thermode temperatures of between 0 and -5°C . The precise time and temperature required varied between experiments depending on the closeness of apposition of the cooling surface to the cord. The block was regularly maintained for up to 45 min and repeated several times in a single experiment. Provided that the temperature of the cord was not allowed to fall below that at which cold block was initially achieved, there was no indication (from the cord dorsum potential) of permanent damage to the cord.

The effectiveness of the cooling procedure in blocking conduction of impulses through the spinal cord was assessed by stimulating the dorsal columns at C2 and monitoring (1) the cord dorsum potential, and (2) the antidromic activity of the single PSDC unit under study. Examples of records made at various stages in the cooling procedure are shown in Fig. 2. Neither the cord dorsum potential nor the antidromic impulse were consistently more sensitive to cooling than the other: the first potential to fail varied between different units in the same experiment presumably reflecting the different depths of PSDC axons in the dorsal columns. Cooling of the cord was therefore continued until both the cord dorsum potential and antidromic single-unit activity were abolished. At this point it was presumed that at least the dorsal half of the spinal cord was blocked.

Cutaneous stimuli

The hair on the hindlimbs was clipped and the cutaneous receptive fields of identified PSDC units mapped in detail using both light tactile and noxious stimuli. Light tactile stimuli were applied using a variety of blunt hand-held probes, air jets and a motorized brush. Noxious stimuli

(i.e. stimuli painful to the investigator) were applied in both mechanical and thermal forms: a maintained noxious pinch was produced by a clip applied to a skin fold, while noxious radiant heating was produced by a halogen lamp with an integral focusing reflector (Beck, Handwerker & Zimmerman, 1974; Fitzgerald & Lynn, 1977). The radiant heating produced a ramp increase in skin surface temperature to a maximum of between 50 and 55 °C over a period of about 8 s, at

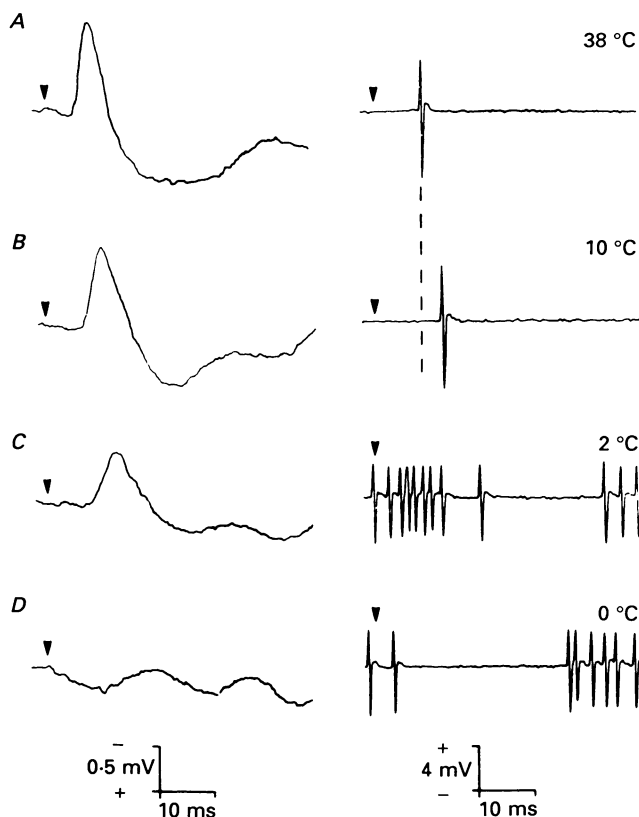


Fig. 2. Assessment of the block of impulse conduction through the spinal cord. Each pair of traces represents a cord dorsum potential recorded at L7 (left) and a single-unit recording from a PSDC axon (right). The records show the progress of the cooling process from prior to cooling (*A*) through to completion of the block (*D*); the temperature of the surface of the cord is indicated beside each pair of records. The arrow-heads mark the point at which a stimulus was applied to the dorsal columns at C2; note the progressive increase in the latency of the cord dorsum potential (*A*–*C*) and of the antidromic impulse in *B*. The single-unit activity in *C* and *D* represents background activity which generally increased in the cold-blocked state. All traces are of single sweeps.

which point the stimulus was terminated. Similar paradigms have been shown to be effective in exciting thermal nociceptive afferent fibres (Georgopoulos, 1976; Kumazawa & Perl, 1977) but do not produce visible signs of injury, provided that the heating is not repeatedly applied at the same skin location. In the present experiments, noxious stimuli were generally applied only twice at each of the skin positions; that is once before and once during the block of descending impulses. To enable stimuli to be accurately repeated at the same skin location before and during cold block of the cord, the stimulus sites were marked on a photograph of the cat's hindlimb. All responses were recorded on magnetic tape and analysed on- and off-line. Discharge frequency histograms were prepared using a computer (Cromenco Systems III).

RESULTS

Recordings were made in the lumbar dorsal columns from the ascending axons of PSDC neurones with cutaneous receptive fields on the ipsilateral hindlimb. Nineteen of these units were successfully recorded for a duration sufficient to allow complete investigation of their receptive field properties both before and during a block of descending activity in the spinal cord.

The sample of units

The receptive field properties of the nineteen units forming the present sample, when analysed before the cold-block procedure, were found to be representative of those reported in previous studies of identified PSDC neurones in chloralose-anaesthetized animals (Brown *et al.* 1983; Noble & Riddell, 1988). The sample consisted of eleven units with receptive fields (excitatory and inhibitory) confined to hairy skin, three units with receptive fields confined to glabrous skin and five units with receptive fields including both hairy and glabrous skin. Sixteen of the units received convergent low- and high-threshold excitatory inputs (that is, they responded to both light tactile and noxious stimuli) and eleven of the nineteen units had inhibitory receptive fields. The conduction velocities of the nineteen axons, measured between the stimulating electrode on the cervical dorsal columns and the lumbar recording site, were between 17 and 62 m s⁻¹; within the ranges reported in previous studies for larger samples of PSDC axons (Angaut-Petit, 1975; Noble & Riddell, 1988).

*Changes in the properties of PSDC neurones produced by block of descending impulses in the spinal cord**Effect on background activity*

All nineteen PSDC neurones investigated had a background activity, even before manipulation of the receptive field. The discharge pattern typically consisted of high-frequency (> 800/s) bursts of activity (four to twelve impulses) interspersed with single, or less commonly, pairs of action potentials. A comparison was made of the level of activity of each of the nineteen units before and during cold block of the cord. Background activities were recorded over periods of 1–2 min following the minimum manipulation of the receptive field necessary to identify the PSDC unit, and again over a similar period immediately the cold-block procedure was judged to be fully effective.

The averaged levels of activity recorded before cold block of the cord ranged between 0.9 and 22.6 impulses/s. The activity of fifteen of the nineteen units increased during cold block of the cord by from 3 to 104 impulses/s; representing increases of between 1.7 and 18.7 times the initial background level. Increases in activity were not obviously correlated with the initial level of discharge, nor were large increases associated only with those units with receptive field properties clearly modified by the cold block.

Two of the nineteen units had reduced background activities in the spinal state

and the discharges of a further two units were virtually unchanged. These units were not of any particular type and were not unusual in any other respect. Indeed three of these units responded to noxious radiant heat only in the cold-blocked state (see below).

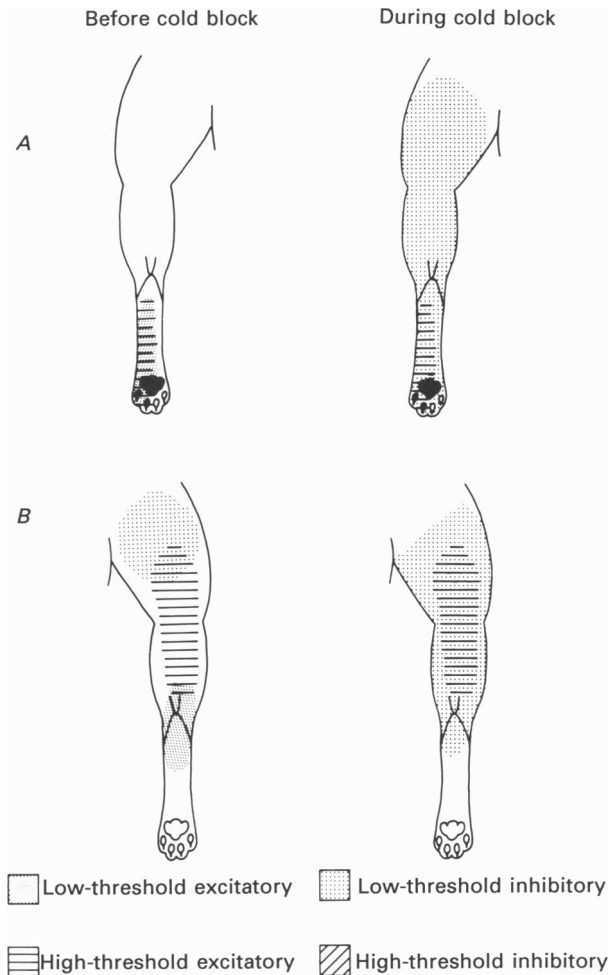


Fig. 3. Effect of blocking descending impulses on the organization of low-threshold cutaneous input to two PSDC units, *A* and *B*. On the left are shown the receptive field components of the two units mapped before cold block of the cord. On the right are shown the receptive fields of the same units during cold block of the cord. Pads from which noxious pinch produced excitatory responses are shown filled; other shadings appear in the key.

Effect on excitatory receptive fields

Low-threshold components

Before cold block of the cord all nineteen PSDC units investigated could be discharged by light brushing and tapping of skin of the ipsilateral hindlimb. For the majority of units cold block of the cord produced few detectable differences in either

the nature of the response to light tactile stimuli or the area of skin forming the low-threshold excitatory field. However, two units were exceptional in this respect; though initially both were discharged by light brushing of an area of hairy skin, during cold block of the cord light tactile stimulation within the same area of skin produced inhibition. The receptive fields of each of these units, mapped both before and during cold block of the cord, are shown in Fig. 3. The modified responses were produced in one unit (Fig. 3A) by the appearance of previously undetected inhibitory input and in the other (Fig. 3B) by expansion of a previously restricted low-threshold inhibitory component.

High-threshold components

All nineteen PSDC units were investigated for their response to sustained noxious pinch both before and during cold block of the spinal cord and eleven units were further investigated for their response to noxious radiant heat. In general, interruption of descending impulses enhanced the responsiveness of units to these noxious forms of stimuli.

Noxious mechanical stimuli. When investigated before cold block of the cord, sixteen of the nineteen units responded with a slowly adapting discharge to a sustained noxious pinch of the receptive field. All of these units remained responsive in the cold-blocked state and an additional unit, previously unresponsive, could be weakly excited by pinch of a single toe pad. Eleven of the sixteen units excited by noxious pinch before cooling of the cord responded more vigorously when the same clip was applied to the same skin position within the receptive field, even after increases in background discharge had been taken into account. An example of one such unit is shown in Fig. 4.

Eight of the sixteen units excited by noxious pinch before cooling of the cord responded during the cold block from areas of skin outside those from which such stimuli were previously effective; that is they responded from a larger area of skin (Fig. 5). Units for which expanded receptive fields were observed included both those with receptive fields restricted to hairy skin and those with receptive fields including glabrous skin. The high-threshold mechanoreceptive components of two units, which were previously restricted to hairy skin, expanded to include glabrous skin of the toe pads.

Noxious thermal stimuli. Of the eleven PSDC neurones investigated before cooling of the cord for responses to noxious radiant heat only four were excited. However, in common with the effect of cooling on responses to noxious mechanical stimuli, block of descending activity enhanced the responsiveness of PSDC units to noxious thermal stimuli. During cold block of the cord three of the four units previously excited by noxious radiant heat responded more vigorously to radiant heat applied to the same skin positions and two responded also from a larger area of skin (Fig. 6). The most striking observation of all, however, was that five of the seven units previously unresponsive to noxious heating were clearly excited during block of descending impulses. An example of one of these units is shown in Fig. 7.

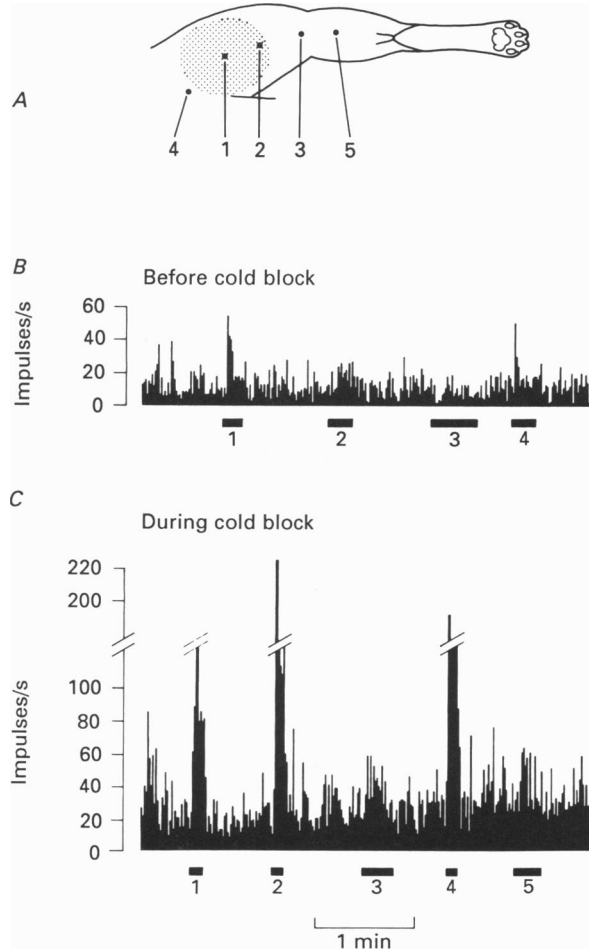


Fig. 4. Effect of blocking descending activity on the responsiveness of a PSDC unit to noxious pinch. *A*, outline of a cat hindlimb on which is shown the low-threshold excitatory component (shaded area) of the receptive field of the unit. The locations at which noxious pinch was applied to the skin are labelled 1–5. A low-threshold inhibitory field has been omitted for clarity. *B* and *C* show discharge frequency histograms for periods of recording made before and during a cold block of the cord respectively. Comparison of these records illustrates the enhanced responsiveness to sustained noxious pinch (bars) produced by cold block of the cord. Note also the increase in background activity. The bin width in this and all subsequent discharge frequency histograms is 1 s.

Effect on inhibitory receptive fields

Low-threshold inhibitory components

Eighteen of the nineteen PSDC units were tested for inhibitory input, evoked by light brushing of skin of the ipsilateral hindlimb, both before and during cold block of the spinal cord. Before cold block, nine units were found to have low-threshold inhibitory areas. Changes in the effectiveness of this light tactile inhibitory input produced by cold block were difficult to assess because of increased background

activity against which any inhibitory input is likely to be more readily apparent. However, all nine of those units with low-threshold inhibitory fields prior to block were at least as readily inhibited when the motorized brush was reapplied to the same area of skin in the spinal state (Fig. 8). Simultaneous movement of many hairs (and possibly other cutaneous receptors) was required to evoke an effective inhibition of

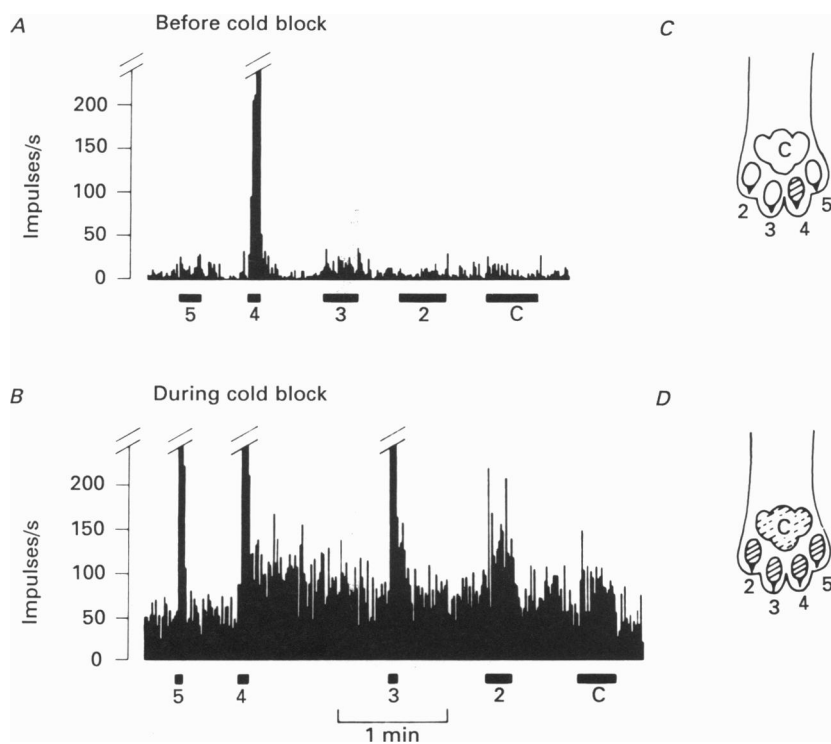


Fig. 5. Effect of blocking descending activity on the high-threshold mechanoreceptive field of a PSDC unit. *A* and *B* show discharge frequency histograms for periods of recording made before and during a cold block of the cord respectively. Comparison of the recordings illustrates the expansion of the area of glabrous skin from which this unit could be excited by sustained noxious pinch (bars) during block of descending activity. Note also the increased background discharge. *C* and *D* are outlines of a cat hindpaw on which are shown the extents of the high-threshold mechanoreceptive field (hatched) before (*C*) and during (*D*) cold block of the cord.

background activity. Since this necessitated repeated stroking of an area of skin of several square centimetres, accurate mapping of small changes in inhibitory areas was not possible. However, the low-threshold inhibitory area of one unit was clearly expanded in the spinal state since it occupied an area of skin from which light tactile stimuli had previously excited the unit (see earlier and Fig. 3*B*). A further four units developed low-threshold inhibitory areas which had not previously been detected; one of these also covered an area of skin from which excitatory responses were previously produced by brushing (Fig. 3*A*).

High-threshold inhibitory components

PSDC units were investigated for high-threshold inhibitory input from skin of the ipsilateral limb both before and during cold block of the spinal cord. Eighteen units were tested for their response to noxious pinch and eleven units further investigated for their response to noxious radiant heat. Before cooling, two units were inhibited

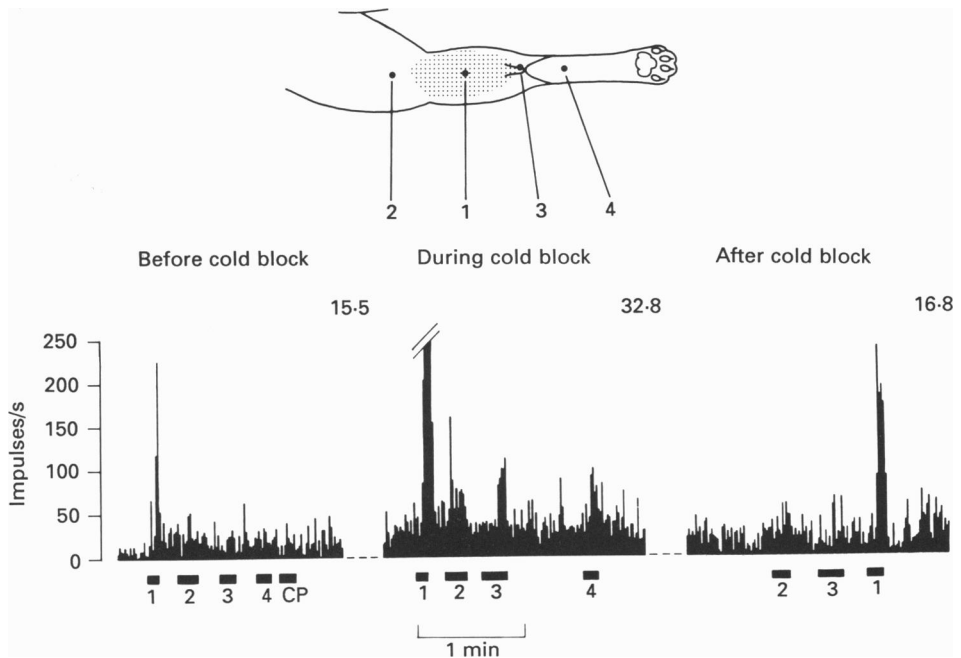


Fig. 6. Effects of blocking descending activity on the high-threshold thermoreceptive field of a PSDC unit. Top, outline of a cat hindlimb on which is shown the low-threshold excitatory component (shaded area) of the receptive field of the unit. The locations at which noxious radiant heat was applied to the skin are labelled 1-4. A low-threshold inhibitory field has been omitted for clarity. Below are shown discharge frequency histograms for periods of recording made before, during and after cold block of the cord. The numbers above each histogram indicate the level (impulses/s) of background activity at each stage. Comparison of the records illustrates the expansion of the area of skin from which this unit could be excited by noxious radiant heat (bars) during block of descending activity (middle record). Also the contraction of the receptive field to its original size after recovery from the cold block (right-hand record). CP, central pad.

by both noxious pinch and radiant heat applied to glabrous skin of toe or foot pads. During cold block of the cord a further two units, for which inhibitory input had not previously been apparent, could also be inhibited by noxious stimuli; one by noxious pinch (radiant heat not tested), and the other by both noxious pinch and heat. One of these units is illustrated in Fig. 9.

*Control observations**Reversal of the cold block*

Reinvestigating the responses of PSDC units after reversing the effects of the spinal cold block would represent the ideal control for the present observations, since

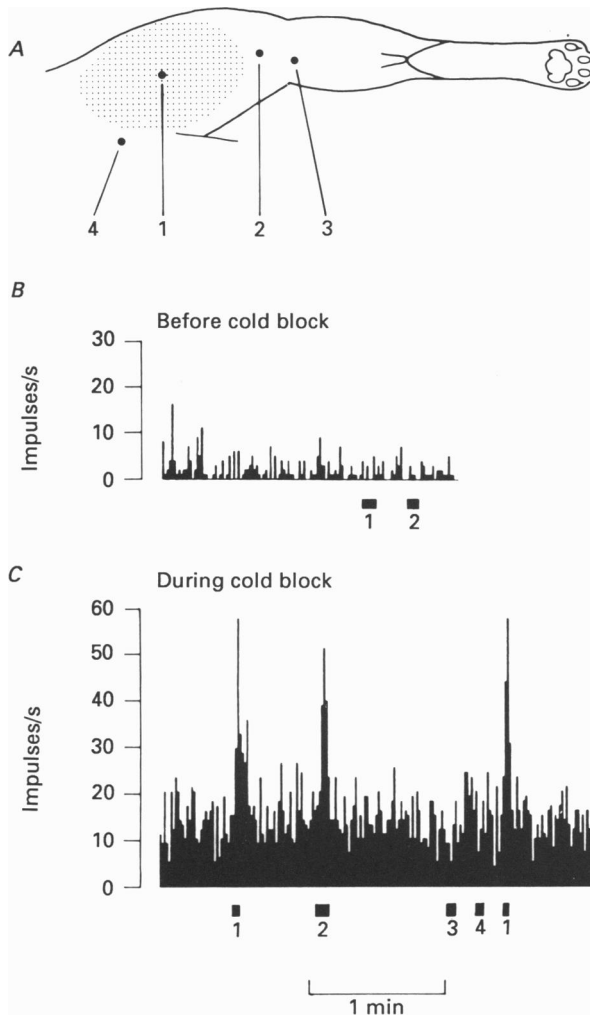


Fig. 7. Effects of blocking descending activity on the responsiveness of a PSDC unit to noxious thermal stimuli. *A*, outline of a cat hindlimb on which is shown the low-threshold excitatory field of the unit. The locations at which noxious radiant heat was applied to the skin are labelled 1–4. *B* and *C* show discharge frequency histograms for periods of recording made before and during cold block of the cord respectively. Comparison of the records illustrates the excitatory responses to noxious heat which became evident only upon block of descending impulses.

such a procedure could provide evidence that the modified response properties observed during cold block of the cord were a direct result of the interruption of descending activity. However, it proved difficult to obtain stable recordings of a sufficient duration to enable such observations to be routinely made.

Recovery from cold block was judged to have occurred when the cord dorsum potential recovered its original shape and amplitude and the unit could be antidromically activated with the same latency as before the cold-block procedure. The background activity of three units from which stable recordings were maintained

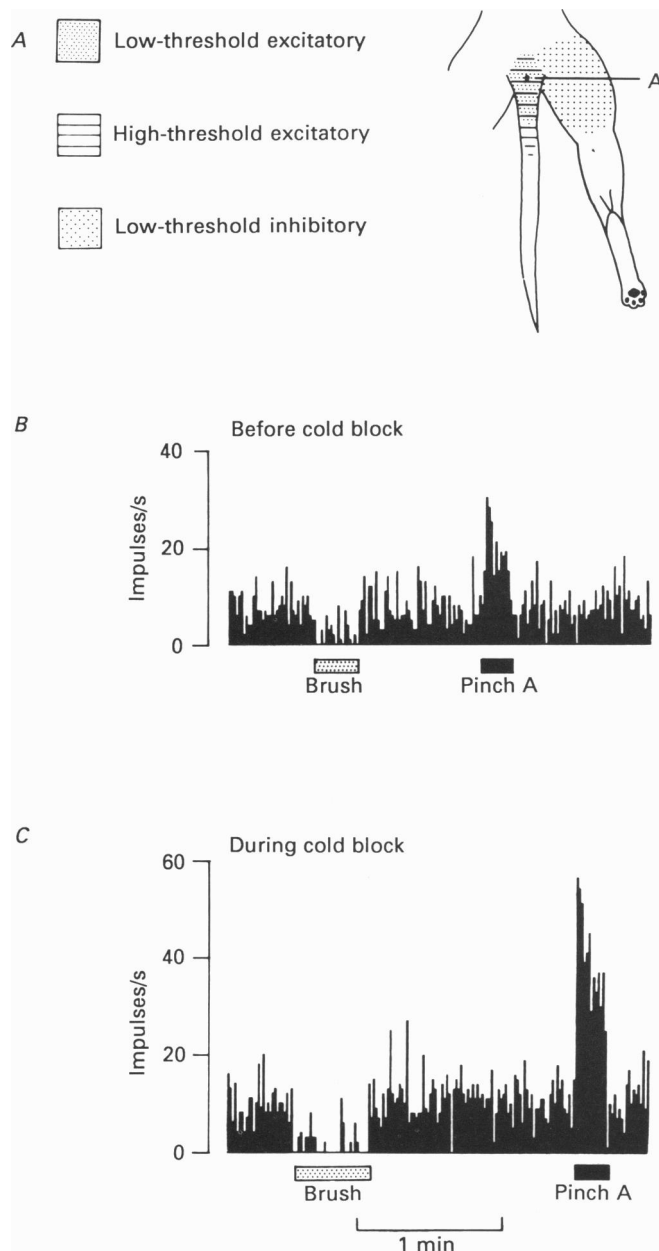


Fig. 8. Effects of blocking descending activity on the low-threshold inhibitory response of a PSDC neurone. *A*, outline of a cat hindlimb on which are indicated the receptive field components of the unit. *B* and *C* show discharge frequency histograms for periods of recording made before and during cold block of the cord respectively. Inhibition of background activity was produced by a motorized brush (stippled bars) applied within the low-threshold inhibitory field. This inhibitory response remained effective during cold block of the cord. A more quantitative comparison of the effectiveness of the inhibition in the two states is prohibited by the increase in background activity that accompanies the cold block.

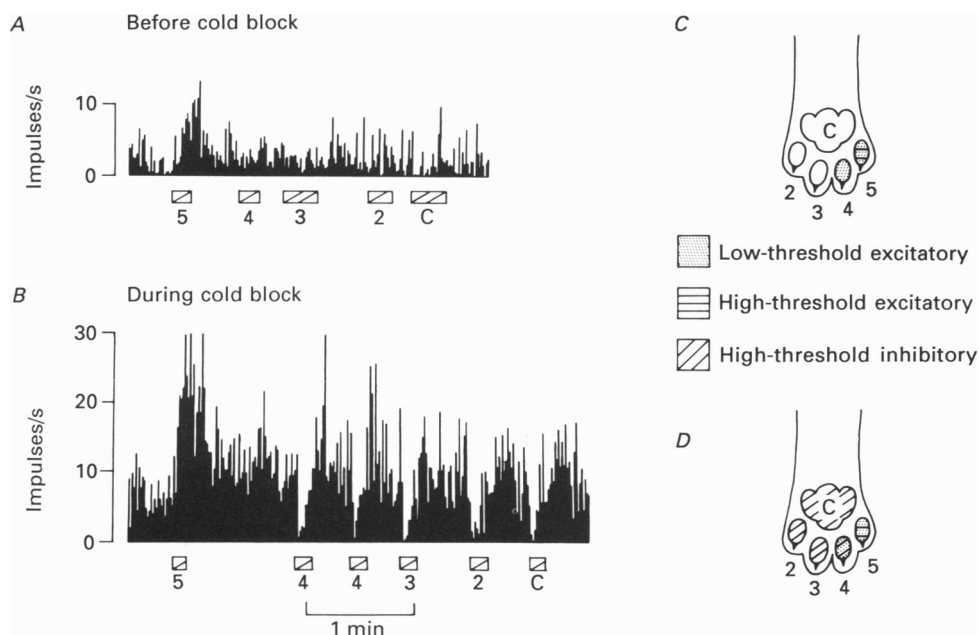


Fig. 9. Effect of blocking descending activity on the high-threshold inhibitory response of a PSDC neurone. *A* and *B* are discharge frequency histograms for periods of recording made before and during cold block of the cord respectively. Comparison of the records illustrates the appearance of a profound inhibition of background activity in response to sustained pinch (bars) of toe and central foot pads. *C* and *D* show outlines of a cat hindpaw on which are indicated the receptive field components of the unit before (*C*) and during (*D*) cold block of the cord.

through the recovery process were investigated. Each had elevated rates of background activity in the spinal state. After recovery from the cold block the rate of activity of two units returned to pre-block levels while that of the remaining unit, though much reduced, had not fully recovered at the time of the analysis. Only one of these units was recorded for a duration sufficient to allow a complete re-analysis of its receptive field properties. During cold block of the cord this unit responded to noxious radiant heat from a larger area of skin than previously. After reversal of the spinalization the responsive area contracted to its original size. These observations are illustrated in Fig. 6.

Additional control observations

The most striking modification of the response properties of PSDC units produced by cold block of the cord, was the appearance of an excitatory response to noxious radiant heat from units which were previously unresponsive. Because of the problem of maintaining a stable recording following recovery from cold block, additional control observations of an alternative form were made. Recordings were obtained from five PSDC units in three cats which were selected for their lack of response to noxious radiant heat. They were tested in the usual manner by applying the radiant

heat to a number of skin positions including some which overlapped areas of skin from which the unit could be excited by pinch. After 8–10 min which is the usual period required to produce a cold block of the cord, each of the five units were tested again at the same skin positions. All of the five units remained unresponsive to noxious heat.

DISCUSSION

The main aim of the present study was to investigate the influence of descending systems on the receptive field boundaries of PSDC neurones. Previous studies (Wall, 1967; Hillman & Wall, 1969) have reported that the receptive field geometries of certain unidentified dorsal horn neurones (recorded in decerebrate cats) are altered by cold block of the cord. The changes observed involved an expansion of both the light tactile and high-threshold excitatory field components, accompanied by a suppression of inhibition from adjacent inhibitory fields.

In the present experiments no obvious expansion of the light tactile components of PSDC neurones could be detected. Indeed, with the exception of two units, low-threshold excitatory areas appeared unaffected by the cold-block procedure. In contrast, both the sensitivity of PSDC neurones to noxious stimuli and the area of skin from which they could be effectively excited by such stimuli were found to be profoundly modified by descending activity. Two-thirds of the units responded more vigorously to noxious mechanical stimulation of the receptive field when descending impulses were blocked. In some units descending inhibitory actions were sufficient to completely suppress thermal nociceptive input; responses to a noxious radiant heat stimulus becoming evident only when spinal conduction was blocked. Furthermore, the high-threshold excitatory components of half the PSDC neurones in the present sample were found to expand in area during cold block of the cord. This is likely to be an underestimate since the stimulus locations used to assess receptive field size were separated by between 2.0 and 3.0 cm so that in some cases changes smaller than this may not have been detected. In addition, for those units which were responsive to thermal stimuli, the expanded receptive field could be confirmed using noxious radiant heat, a stimulus which avoids the possibility of exciting sensitive mechanoreceptors at a distance. It is unlikely that these substantial modifications of receptive field properties could be explained by the sensitization of nociceptors (Burgess & Perl, 1967; Beitel & Dubner, 1976; Croze, Duclaux & Kenshalo, 1976; Fitzgerald & Lynn, 1977) since noxious stimuli were not generally applied to a single receptive field location more than once in each state. This view is supported by the control observations in which PSDC neurones, initially unresponsive to noxious heat, remained so when noxious stimuli were repeated but in the absence of cold block.

Little is known about the interaction of descending systems with segmental inhibitory processes. Furthermore, there are conflicting reports of the effect of cold block on cutaneous inhibitory fields of dorsal horn neurones. Hillman & Wall (1969), have reported that the light tactile inhibitory zones of 'lamina V-type' neurones are almost completely suppressed during cold block of the cord, whilst Brown (1971) has reported that inhibition of spinocervical tract cells, whether by 'light tactile or noxious stimuli, is more easily elicited in the spinal state. In the present experiments, inhibition from both low- and high-threshold inhibitory field components, detected

under conditions of normal spinal conduction, remained effective when descending impulses were blocked. A direct comparison of the efficacy of inhibitory actions in the two states was complicated by the increased levels of background discharge in the cold-blocked state, against which inhibition is more easily observed. However, some evidence for enhanced inhibitory actions was obtained: the light tactile excitatory regions of two PSDC units shrank during cold block of the cord as a result of the appearance or expansion of light tactile inhibitory components, and two units developed high-threshold inhibitory responses which had not previously been detected. Clearly then the cutaneous inhibitory fields of PSDC neurones do not depend on a supraspinal loop for their actions and there are some indications that their effectiveness may be modulated by systems descending from the brain.

The effects described in the present study are likely to result from the actions of several descending systems; the cold-block technique interrupts descending fibres in at least the dorsal half of the spinal cord but can of course only reveal the actions of those systems which are tonically active in an animal prepared for electrophysiological recording. Tonic descending inhibition of spinal reflex pathways in the *decerebrate* cat has been shown to originate at least in part from the raphe and juxtarraphe regions of the medial reticular formation (Engberg, Lundberg & Ryall, 1968), while tonic descending inhibition of dorsal horn neurones in the *barbiturate-anaesthetized* cat emanates largely from the brain stem lateral reticular formation (Hall, Duggan, Morton & Johnson, 1982; Morton, Johnson & Duggan, 1983). Though some differences in the descending systems responsible for tonic control of dorsal horn neurones and transmission in spinal reflex pathways may exist, these contrasting results also raise the possibility that tonic descending influences might originate from largely separate descending systems in anaesthetized and decerebrate preparations. This possibility should be considered when comparing the results presented here, from the chloralose-anaesthetized cat, with previous studies of tonic descending influences on the receptive field organization of dorsal horn neurones, all of which have used decerebrate preparations (Wall, 1967; Hillman & Wall, 1969; Brown, 1971).

The normal physiological circumstances under which descending regulatory mechanisms are active remain largely unknown. There has long been speculation concerning their role in the control of sensory processing, particularly in relation to the perception of pain under different conditions (Hagbarth & Kerr, 1954; Wall, 1979). In this context, recent experiments in conscious monkeys (Hayes, Dubner & Hoffman, 1981) suggest that both the sensitivity and receptive field size of dorsal horn neurones responding to noxious thermal stimuli are modulated in freely moving animals according to their attentive behaviour. The interpretation of results obtained from anaesthetized acute preparations requires caution; it has been suggested, for example, that tonic descending activity in experimental animals is activated by the trauma of procedures necessary to prepare an animal for electrophysiological recording (Clarke, 1985). Nevertheless, it is clear from the present study that the PSDC system is amongst those somaesthetic pathways under the influence of descending mechanisms which, whatever their precise physiological function, have the potential to modify and regulate the transmission of cutaneous sensory messages.

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